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THE LIFE HISTORY OF THE PIKE-WHITEFISH TAPEWORM

Triaenophorus crassus

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by

RICHARD B. MILLER

A report prepared for the Fisheries Branch,
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The Life History of the Pike-Whitefish Tapeworm, **Triaenophorus crassus**

by R. B. MILLER

The yellowish cysts in the flesh of whitefish and tullibee are, unfortunately, all too familiar to those who have had any connection with the fishing industry in the Prairie Provinces. For the past fourteen years these cysts, although harmless to man, have caused and are still causing economic losses to the fishing industry. The cysts are one stage in the life history of the tapeworm, *Triaenophorus crassus;* they occur throughout the northern hemisphere in the flesh of fishes of the whitefish family and they have been known in Europe since the seventeenth century.

The Alberta Government decided several years ago that a thorough investigation of this parasite should be undertaken with the object of discovering what, if any, control possibilities existed. The author, a member of the Department of Zoology of the University of Alberta, was given this task. Most of the work has been done at the government's whitefish hatchery on Lesser Slave Lake. From time to time, detailed technical accounts of the progress of the work have been published in the Canadian Journal of Research There has been, however, a considerable demand for information of a non-technical nature about this parasite; the present account has been written to try and satisfy this demand. The facts have been taken largely from the author's own reports in the Canadian Journal of Research, but also, in part, from the published works of other investigators, mainly in Europe. Most of the illustrations appear for the first time in this work, but figures 4, 5, 8, 9, 15 and 16 are reproduced from the Canadian Journal of Research.

The author would like to take this opportunity of thanking the Honourable N. E. Tanner, Minister of Lands and Mines, and two members of his Department, E. S. Huestis, Fish and Game Commissioner, and H. B. Watkins, Superintendent of Fisheries, for their interest in and support of this work. Thanks are also due to Professor William Rowan of the Department of Zoology at the University of Alberta who interested Provincial officials in getting the work started.

TAPEWORMS

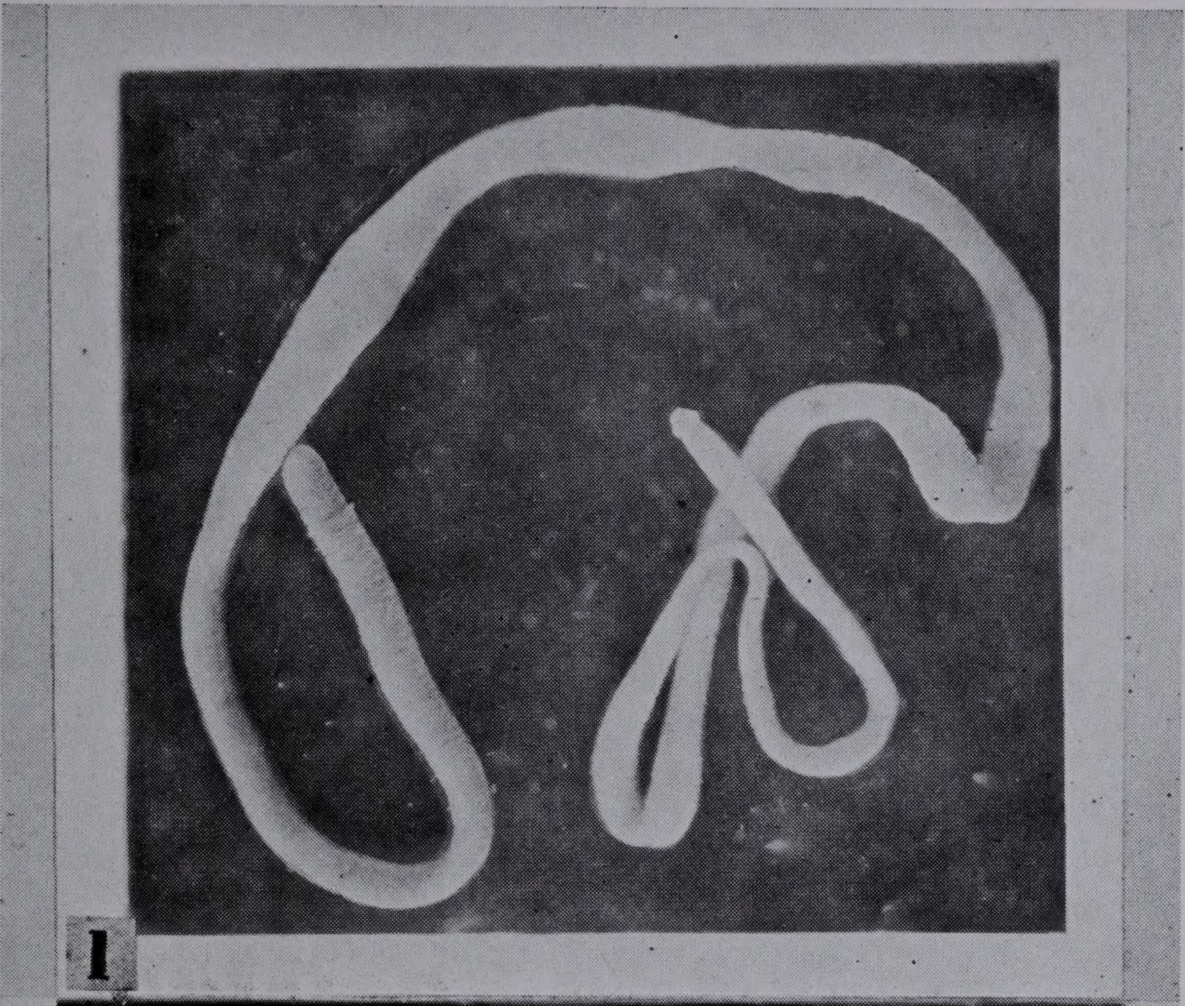
To write a non-technical account of the life history of a tapeworm is an almost impossible task. Such little known animals possess only the names which have been given to them by scientists; no familiar phrases have developed about either their names or the various details of their lives. The terms used in this account, therefore, have had to be largely technical ones since no others were available. Each term has been explained where it is first used with the hope that in this way the account may be readable by any person.

There are a great many different kinds of tapeworms; each kind has special characteristics which distinguish it from the others. A study of these is a specialist's job and a man must spend several years working with tapeworms before he is competent to judge what kind any particular worm may be. But all tapeworms have a number of characters in common and the reader will follow the account of *Triaenophorus crassus* more intelligently if some of these are explained now.

The adult or sexually mature tapeworm is very long and very flat, as the name implies, like a piece of tape; most of them are dead white in colour. At one end of the tape is an organ of attachment called the scolex; this structure usually has suckers and sometimes hooks for fixing the worm to the lining of its host's intestine. One might call the scolex the head were it not for the fact that eyes, ears, nose and mouth, usual parts of a head, are wholly lacking. The rest of the body is called the strobila. It consists of a chain of many identical segments joined together end to end. Each segment contains a complete set of male and female reproductive organs which can perform their functions independent of the other segments. There is little besides the reproductive organs in the segments; only a set of rather weak muscles, a few nerve strands and a simple excretory system. No intestine, mouth or anus is present. These remarkable animals are, therefore, hardly more than animated reproductive organs capable of making sluggish movements. Intestines and blood vessels are unnecessary as the worms live bathed in predigested food which they soak in through their skins. Being deaf, dumb and blind is hardly a disadvantage to a creature which spends its whole adult life in the intestine of another animal.

The animal in whose intestine the tapeworm spends its adult life is called the final host. All varieties of creatures from fishes to mammals harbour tapeworms in their intestines. Most tapeworms have an intermediate host as well as a final. In the intermediate host some immature stage of the life cycle is passed. The intermediate host is usually some animal which is commonly eaten by the final host so that the tapeworm reaches its final host by being swallowed. A few tapeworms have to pass through two intermediate hosts, a first and second, before the adult stage is reached. Such an one is *Triaenophorus crassus;* the final host is the pike or jackfish, the first intermediate host is a small crustacean, *Cyclops bicuspidatus,* and the second the whitefishes—i.e., tullibee and whitefish.

An interesting thing about tapeworms is what is called their *species specificity;* this means that a particular kind of tapeworm can live only in a particular kind of animal. *Triaenophorus crassus* in Alberta can live only in the pike or jackfish. Thousands of ling and pickerel swallow literally millions of cysts but these never become established; they are digested like ordinary food. Only in the jackfish do the worms find conditions just right for their development.



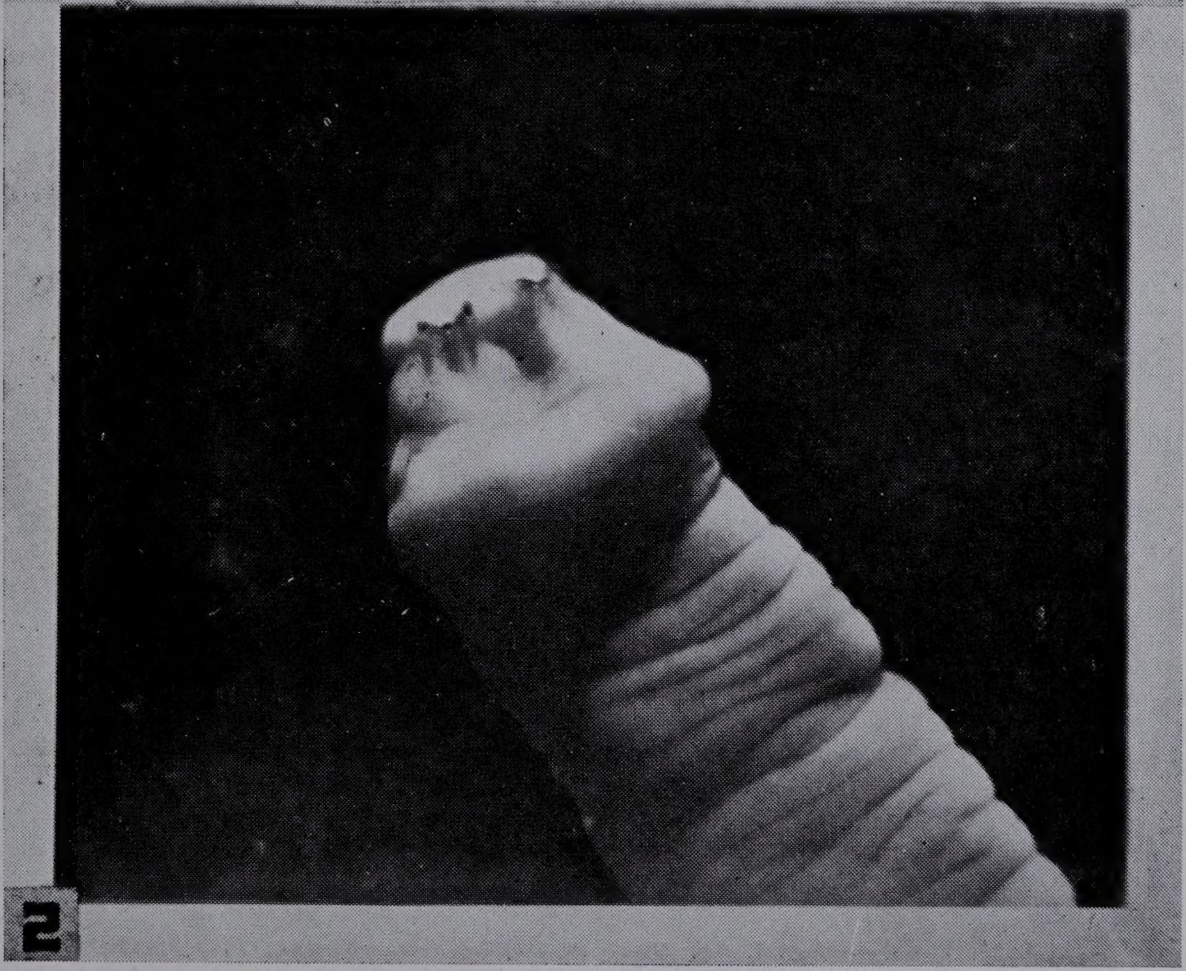


Figure 1. A mature specimen of *Triaenophorus crassus* ready to lay its eggs. The attachment organ, the scolex, is visible at the smaller end. About natural size.

Figure 2. The scolex of the same specimen shown in Figure 1. Enlarged 30 times.

TRIAENOPHORUS CRASSUS IN THE PIKE OR JACKFISH

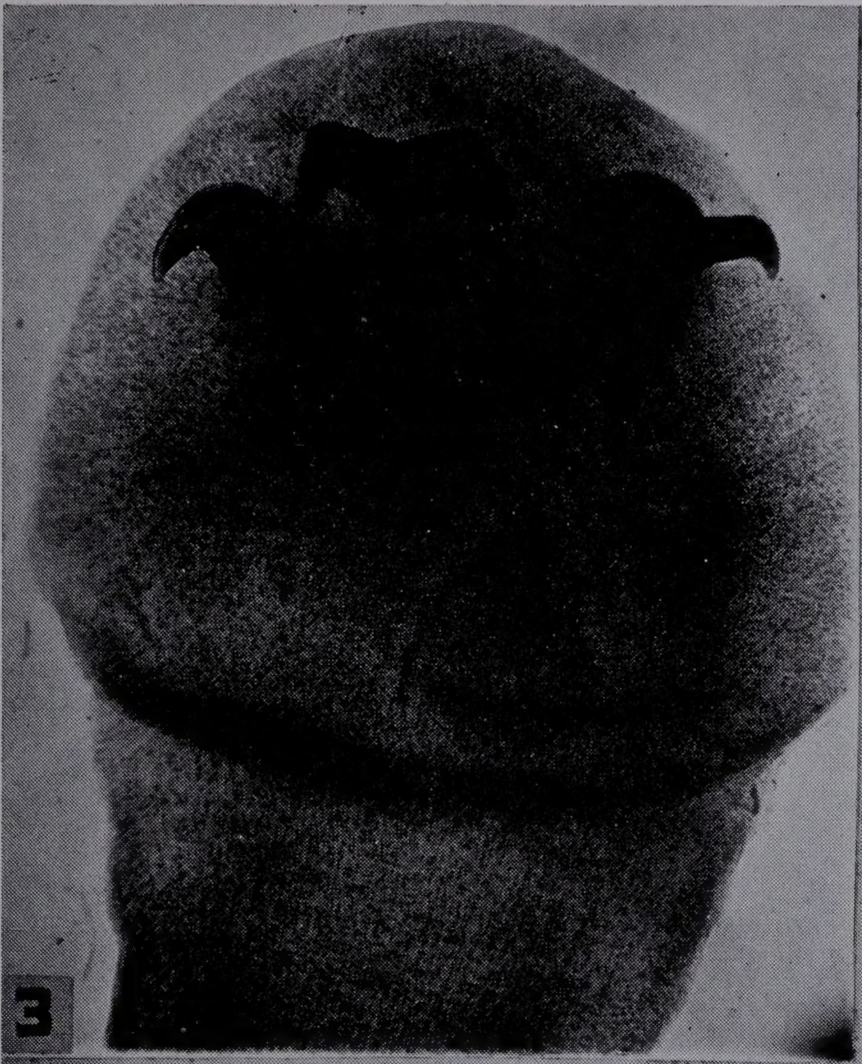
The adult tapeworms live in the intestine of the pike just beyond the stomach. In the summer and early winter they are not very conspicuous and are largely hidden in the slime always present in the intestine. As the winter lengthens and spring approaches the worms grow larger and more noticeable until, by February or March, they form a large white mass completely filling the intestine. Each worm is then from eight inches to over a foot long and nearly a quarter-inch broad at the widest point. The scolex is buried in a deep pit in the intestinal wall, thus anchoring the worm in the intestine. A photograph of a fully grown specimen is shown in Figure 1.

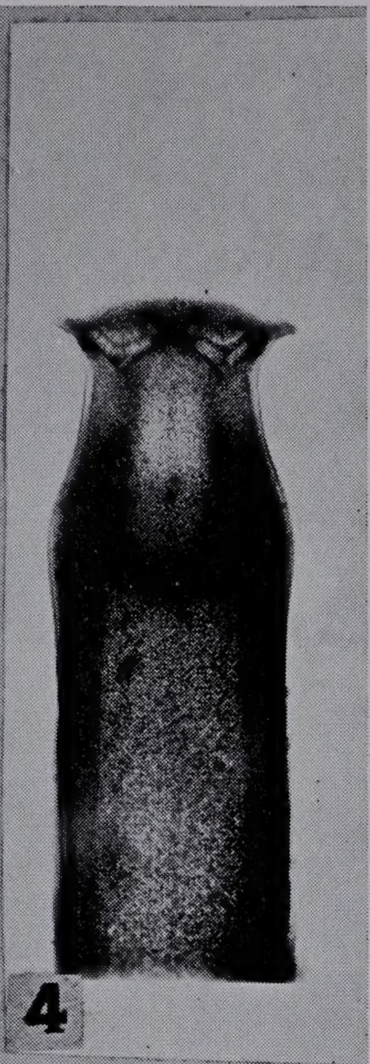
The scolex is a very characteristic structure. It is provided with two rather weak suckers and four large three-pronged hooks. In Figure 2 the scolex of the same worm pictured in Figure 1 is shown magnified making these hooks visible. Figure 3 is a photograph taken through a microscope; it shows a scolex which has been stained and rendered transparent so that the four hooks show very clearly. These hooks are typical of *Triaenophorus crassus* and give an easy and sure means of identifying the worm. A closely related worm, *Triaenophorus nodulosus,* is often found mixed with *crassus* in small pike. It is easily distinguished by its smaller, more slender hooks as shown in the photograph in Figure 4. *T. nodulosus* forms cysts in the livers of young ling and is of no economic importance.

An examination of Figures 5 and 6 shows how the scolex is attached to the pike's intestine. Figure 5 is a photograph of a very thin slice of intestine at the point of attachment of a *T. crassus;* Figure 6 is a diagram of the same thing and serves as a key to the photograph. The worm destroys the intestinal lining (gland layer) and forms a deep pit. The scolex hooks are thrust into the sides of this burrow and hold the worm very firmly in place. It is difficult to pull a live worm out of its pit; usually the body breaks and leaves the scolex buried.

In April the coiled white mass of worms in the pike's intestine begins to straighten out a little and each worm extends, without kinks down the length of the intestine. Toward the end of April these worms, if placed in water, will release clouds of white eggs through a series of pores, one in each segment (Figure 7.) For about two weeks, from the end of April to the middle of May the worms are busy laying eggs. Some of the eggs are released into the pike's intestine to find their way to the lake with the faeces. Others are carried out in bits of strobila which break off and are discharged. At this time of the year fisherman often notice these pieces of worm on the bottoms of fish boxes in which jackfish have been packed.

Egg-laying is the tapeworms last mortal act. Figure 8 is a photograph of a few segments just before egg-laying; Figure 9 is a photograph of a similar group of segments just after egg-laying. The expulsion of the eggs causes the worm to shrink to less than half its former size; it then breaks up, leaves the fish and dies. For a time





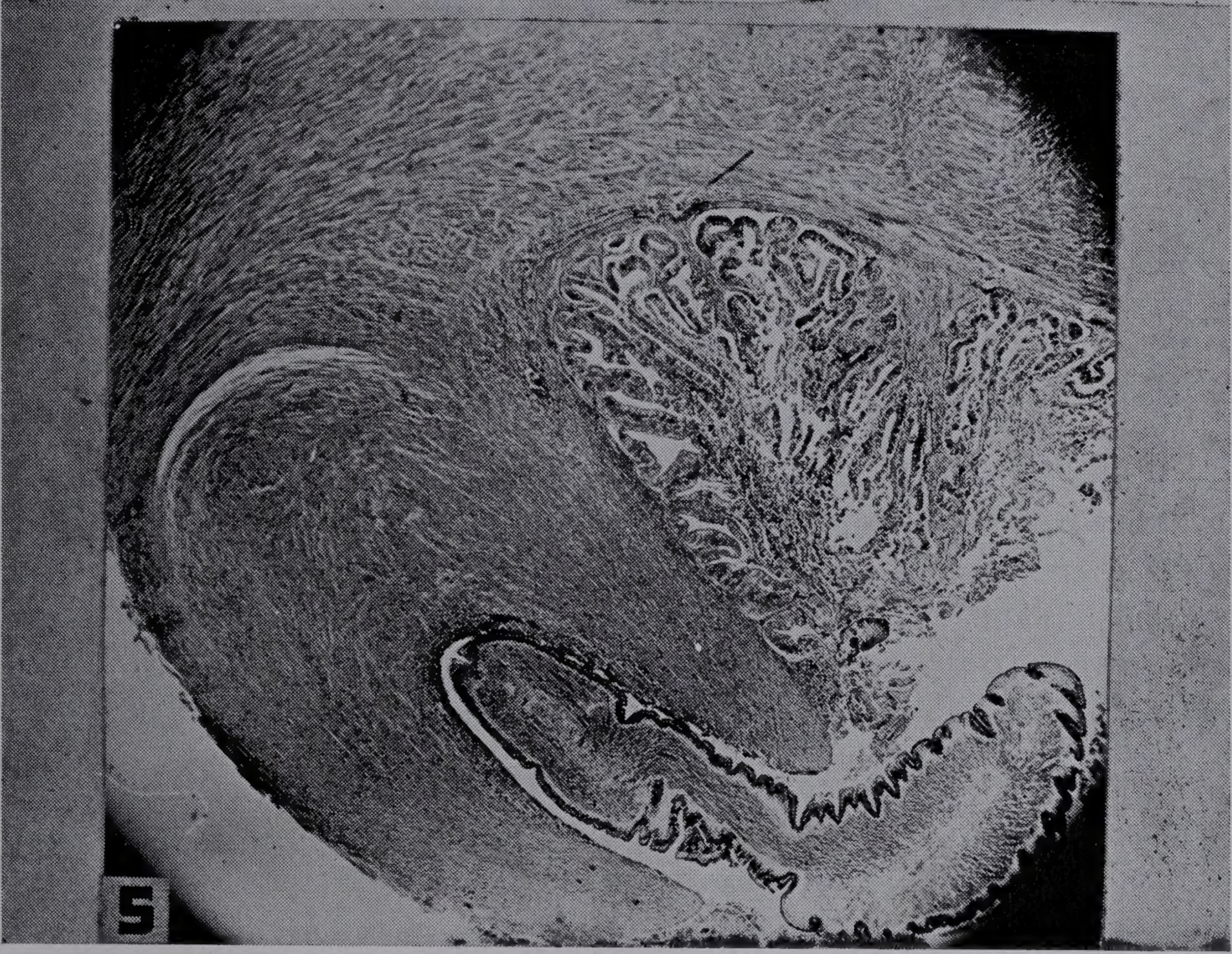
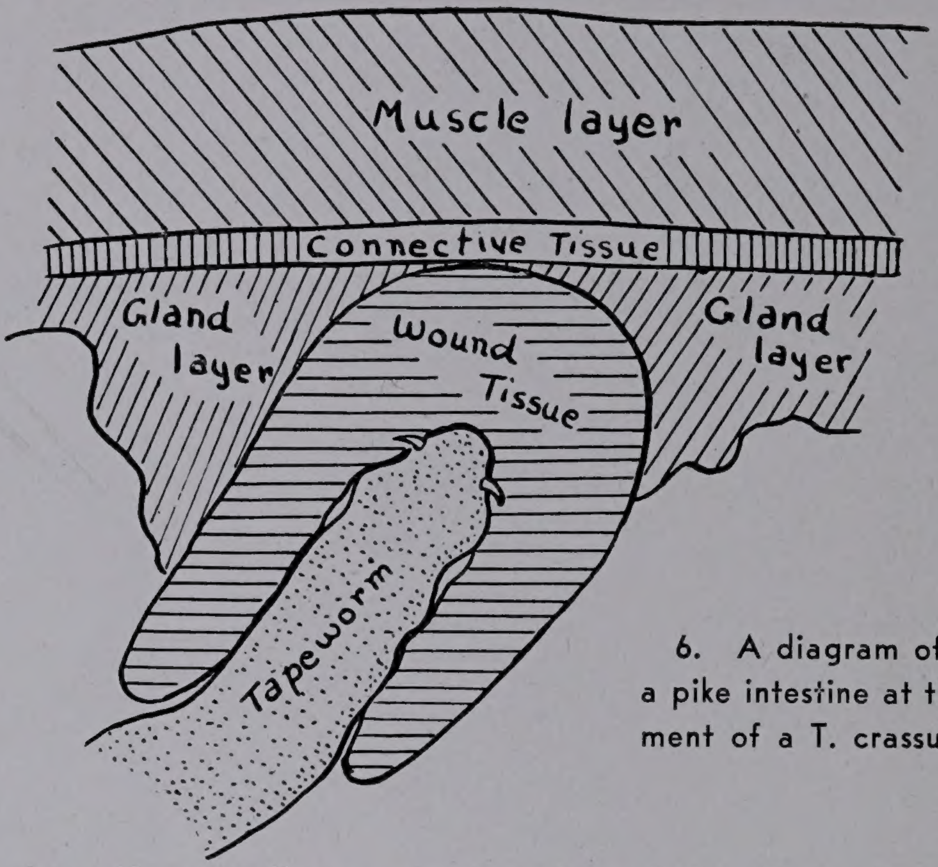


Figure 3. The scolex of *T. crassus* stained and rendered transparent so as to show the four characteristic hooks. Enlarged 70 times.

Figure 4. The scolex of *T. nodulosus,* a closely related tapeworm, treated in the same way. Two of the small, slender hooks are visible. Enlarged 34 times.

Figure 5. A section through the intestinal wall of a pike at the point of attachment of a *T. crassus.* Enlarged 16 times. The key to this photograph is given in Figure 6.



6. A diagram of a section through a pike intestine at the point of attachment of a T. crassus. See Figure 5.

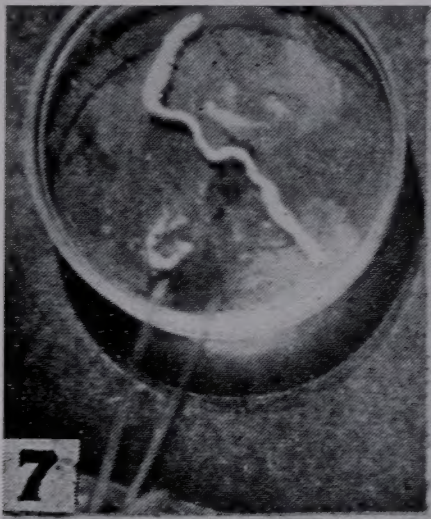
after egg-laying the scolices can be found in the pits in the pike's intestinal wall; these soon drop out and eventually the pits heal over and disappear. *T. crassus* is, therefore, an annual. It dies in the spring after releasing its eggs and the pike are clean for a time. By the end of June small worms, an inch or so long, begin to show in the pike's intestine. These are the new generation of *T. crassus;* they will be ready to spawn by April of the next year, when they too will die and leave their hosts.

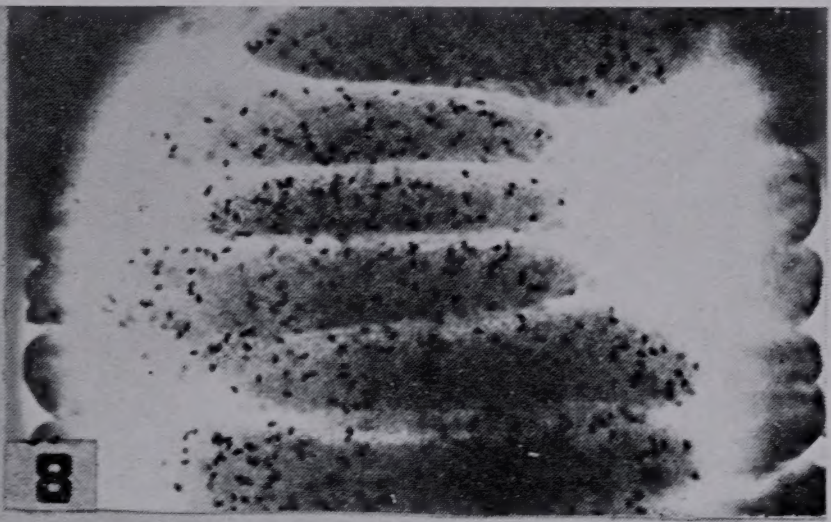
THE EGGS

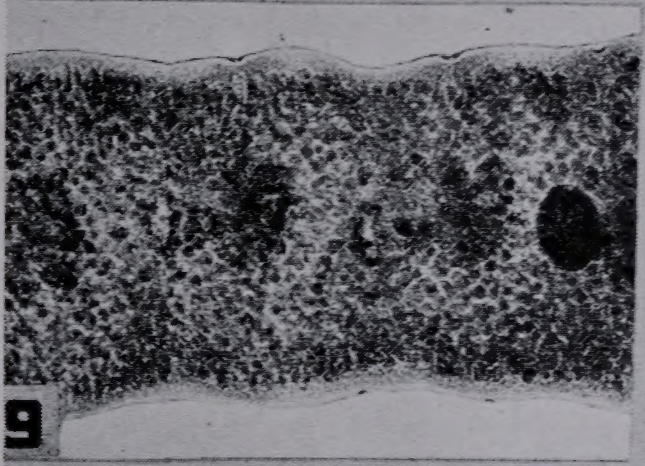
When the eggs of *Triaenophorus crassus* first escape from the vent of the jackfish into the water they are white in colour. They sink and soon turn brown to become invisible on the dark bottom. They are exceedingly small, 0.0024 inches long by 0.0016 inches wide, but are produced in enormous numbers, about one and one-quarter millions from one worm.

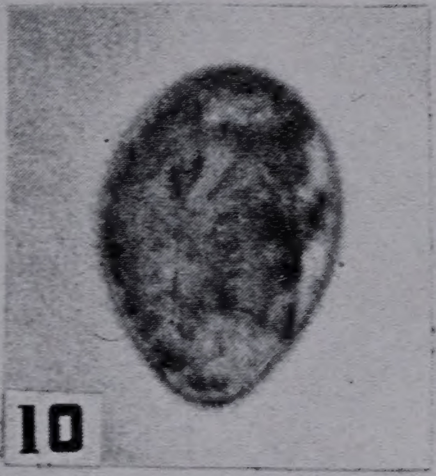
The eggs are shaped like hens' eggs (Figure 10). At the smaller end a tiny cap can just be distinguished under the high powers of a microscope. The shell is transparent and the embryo inside can be clearly seen. This embryo is ready to hatch very soon, sometimes immediately after the egg reaches the water. It moves around inside the shell at first slowly but then faster and faster as the time of hatching approaches. Finally the embryo gathers itsself in a bunch at the larger end of the egg and then hurls itself violently at the little cap on the smaller end. Several such batterings serve to knock the cap open and the embryo squeezes out through the small hole. The cap usually stays attached to the empty egg like an open door. A number of photographs have been made of the eggs in different stages. Figure 10 shows a ripe egg, just before hatching. The upper drawing in Figure 14 is a key to this photograph; the embryo with its six little hooks is shown. Figure 11 is a photograph of a hatched egg to show the open cap at one end. The middle drawing in Figure 14 shows the same thing. Figures 12 and

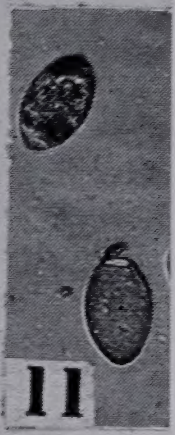
13 are two frames from a moving picture of an egg hatching. The movie was taken through a microscope under very high magnification (about 470 times).

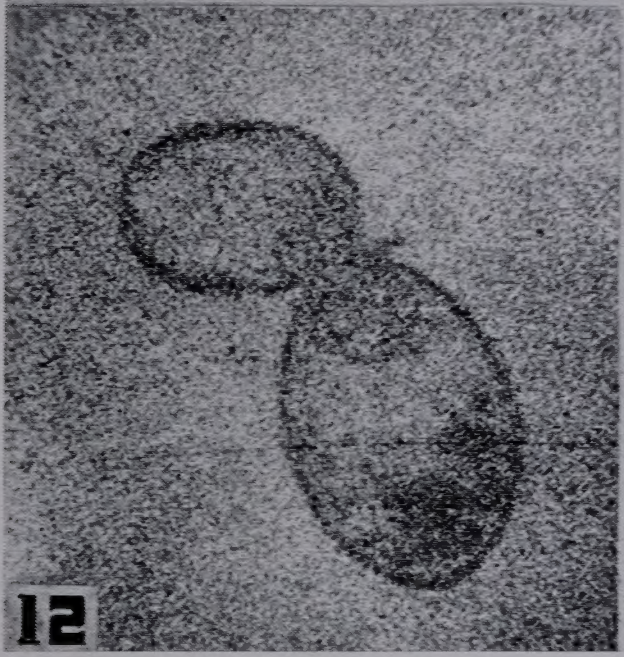












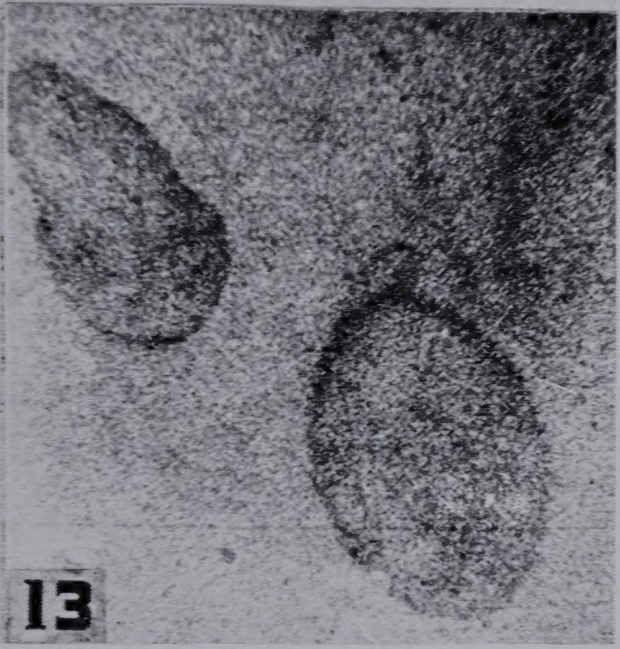


Figure 7. A fragment of a ripe *T. crassus* in a dish of water. The white clouds are eggs escaping from a pore in each segment. About one third natural size.

Figure 8. A portion of a ripe *T. crassus* stained to show the masses of eggs in each segment. Enlarged 17 times.

Figure 9. A similar portion of a spent *T. crassus*. The eggs are mostly gone and the segments have shrunk. Enlarged 26 times.

Figure 10. The ripe egg of *T. crassus*. Enlarged 470 times.

Figure 11. A ripe egg (upper) and a hatched egg (lower). The open cap of the hatched egg can be seen. Enlarged 148 times.

Figures 12 and 13. Two frames from a motion picture of a *T. crassus* egg hatching. In 12 the embryo is still squeezing through the hole in the egg. In 13 it is swimming away. Enlarged 470 times.

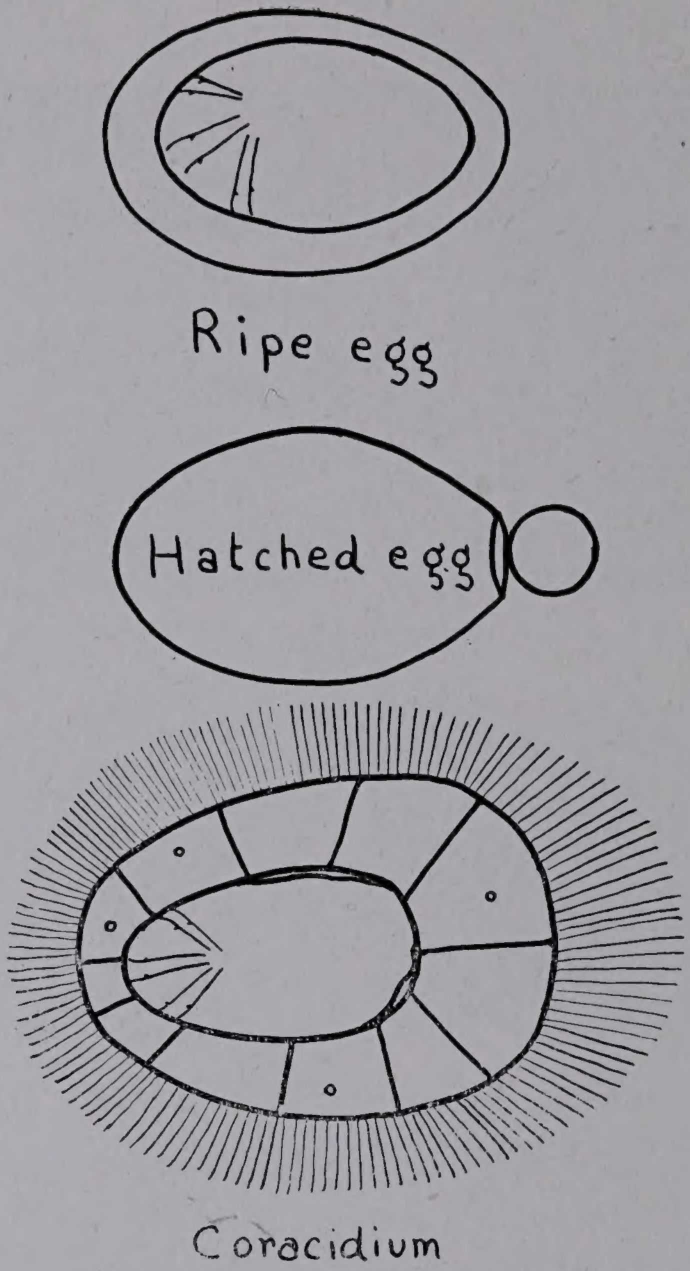


Figure 14. A diagram which serves as a key to Figures 10, 11, 12 and 13. The coracidium is the young tapeworm as it appears several hours after hatching. The fine hair-like structures are the cilia with which it swims.

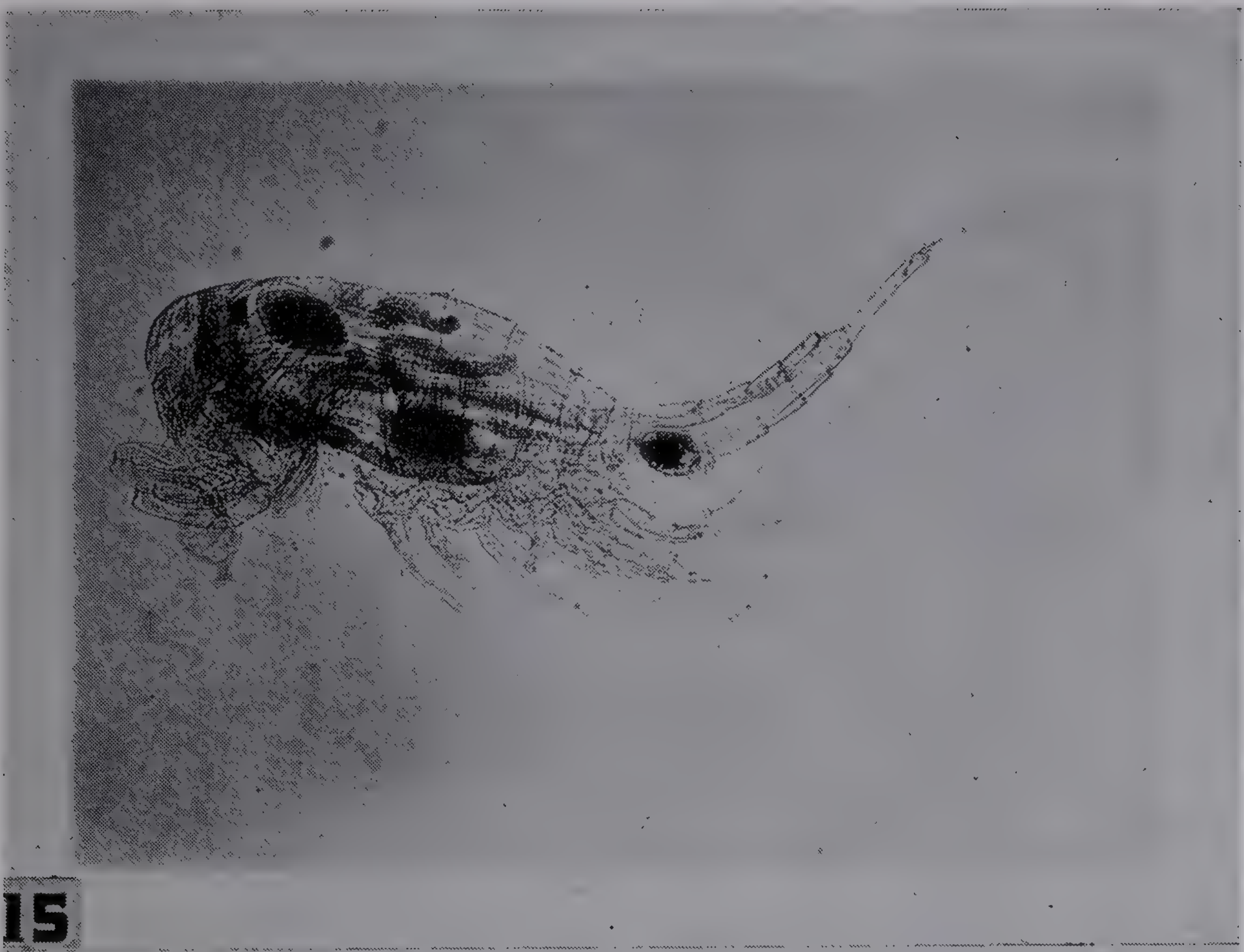
THE CORACIDIA

The tiny embryo which escapes from the egg is called a coracidium. At first it is the same size as the egg but in an hour or two it has swelled to nearly twice the size. The swelling takes place in an outer, transparent, jelly-like coat which absorbs water. This coat is covered with many hair-like projections named cilia which beat in the water and propel the embryo around (Figure 14, bottom drawing). Within the coat is the little embryo with its six hooks still showing clearly.

The coracidia swim around aimlessly for about two days. At the end of this time they sink to the bottom and soon die, unless, of course, they succeed in being swallowed by the proper animal in which to continue their development.

TRIAENOPHORUS CRASSUS IN CYCLOPS BICUSPIDATUS

The identity of the first intermediate host of *T. crassus* was unknown. The only method of learning what animal served this purpose was to put the coracidia in bottles of water along with various small creatures that might be the host. By this trial and error pro-



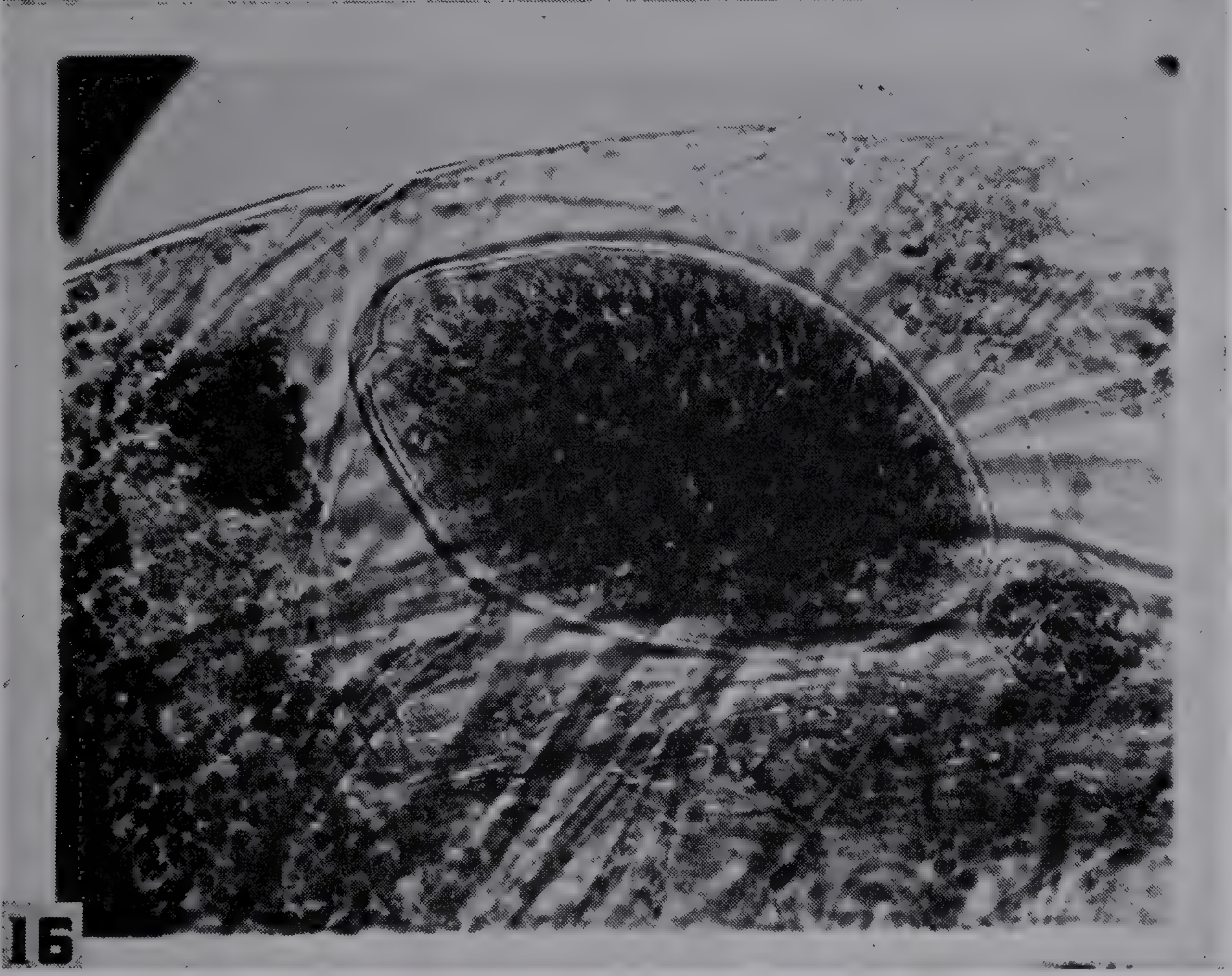


Figure 15. A specially stained and mounted specimen of *Cyclops bicuspidatus,* the first immediate host. It contains two parasites which show as dark patches. Enlarged 60 times.

Figure 16. One of the parasites shown in Figure 15 photographed under higher magnification. At this stage the parasite is called a procercoid. Enlarged 390 times.

cedure it was found that *Cyclops bicuspidatus* was the first intermediate host. A photograph of one of these little animals, enlarged 60 times, is shown in Figure 15. *Cylops bicuspidatus* is a diminutive relative of the lobsters and crabs; he and his kind are sometimes, though not correctly, called waterfleas. They occur in countless millions in the waters of lakes and ponds all over the world. Several kinds of *Cyclops* were seen to swallow the young tapeworms (coracidia) but they survived only in *C. bicuspidatus;* in the others they were digested. *C. bicuspidatus* actively, and evidently purposefully, swallowed the coracidia; apparently the coracidia look like a satisfactory meal to them. Once in the *Cyclops'* stomach the young tapeworms shed their ciliated coats and set about making their way through the stomach wall. They do this by tearing a hole with the points of their hooks. The author has seen as many as thirty coracidia tearing into the stomach wall of one *Cyclops*. The *Cyclops* quivers and jerks with pain and sometimes succeeds in contracting its stomach so as to eject the parasites through its mouth and back into the water.

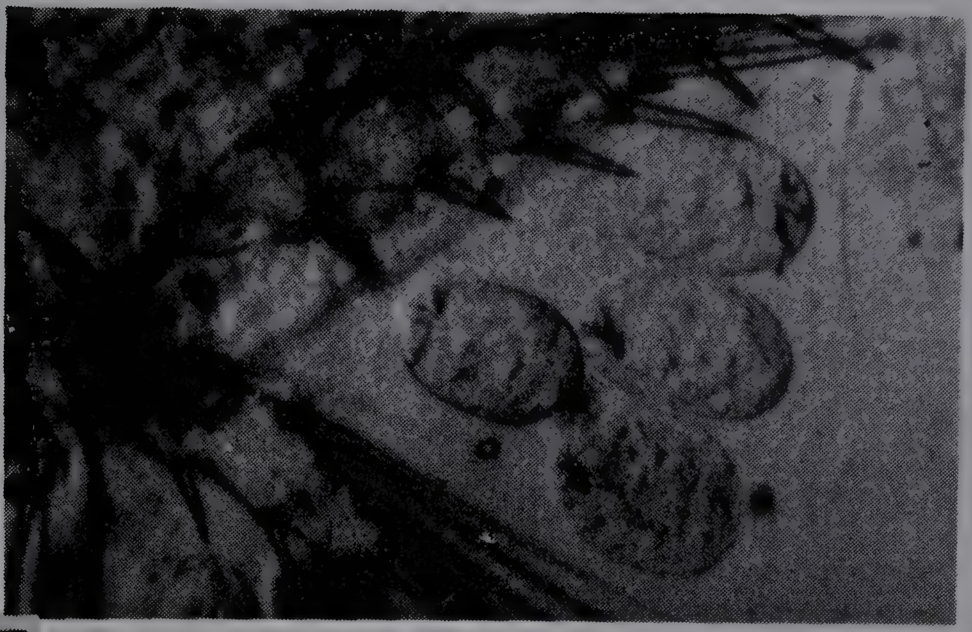
The journey through the stomach wall completed, the parasites settle down in the body cavity of their host for a growth period of ten days to two weeks. Figure 17 shows four of them crushed out of a *Cyclops* two days after they got in. The dark marks at one end of each parasite are the hooks they used to gain their entry. The hooks are never used again; in fact the parasite now proceeds to separate them from the main part of its body in a little blob at the end. While this blob is forming the parasite increases in size; when the hooks are fully separated from the rest of the body the young worms have increased five or six times in length and may occupy much of the space inside the *Cyclops*. The *Cyclops* shown in Figure 15 has two fully grown parasites in it. In Figure 16 one of these is shown photographed under higher magnification. The separate piece with the hooks can be seen. Figure 18 is a photograph of a living parasite of the same age which has been squeezed out of its host.

The stage shown in Figures 16 and 18 takes ten days to two weeks to develop. The parasite is now known as the procercoid and it can develop no further in the *Cyclops*. For continued development the *Cyclops* containing procercoids must be swallowed by a tullibee or whitefish.

The procercoids move about actively in the *Cyclops* but don't seem to bother their host much. In one experiment a *Cyclops* lived thirty days, about a normal life span for such a creature, with several procercoids creeping around in it. Should the *Cyclops* die without being swallowed by a tullibee or whitefish the procercoids die with it.

TRIAENOPHORUS CRASSUS IN TULLIBEE.

The fish commonly known as tullibee throughout the Prairie Provinces are not actually all of one kind. Probably at least four kinds of fish are included in the term tullibee. They all have one



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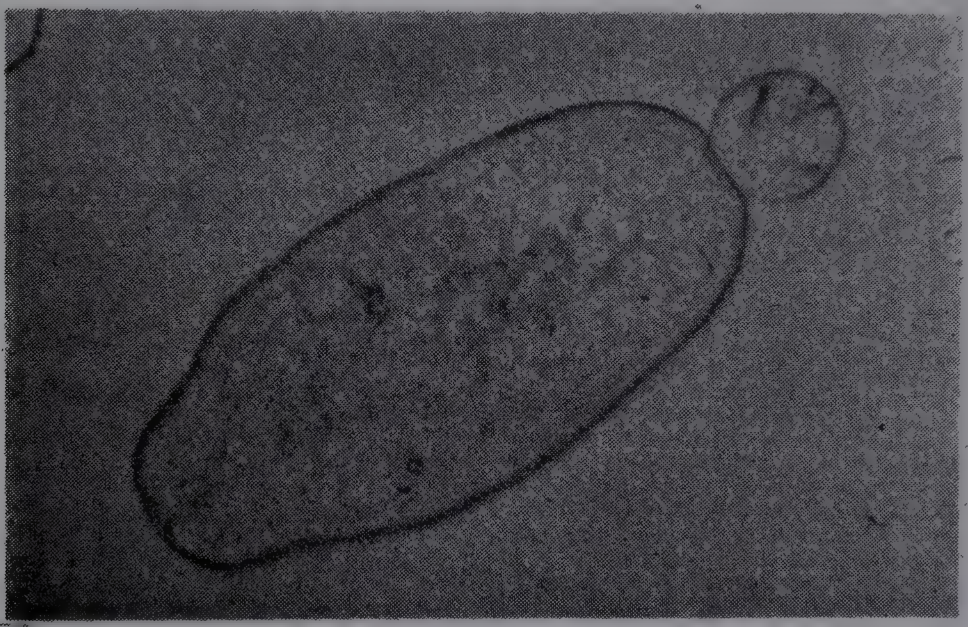

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Figure 17. Four young procercoids squeezed out of a *Cyclops* about two days after their entry. The remains of the *Cyclops* from which they are squeezed show in the photograph. Enlarged 400 times.

Figure 18. A mature procercoid of *T. crassus* photographed while still alive and after being squeezed out of its host. Same stage as Figure 16. Enlarged 400 times.

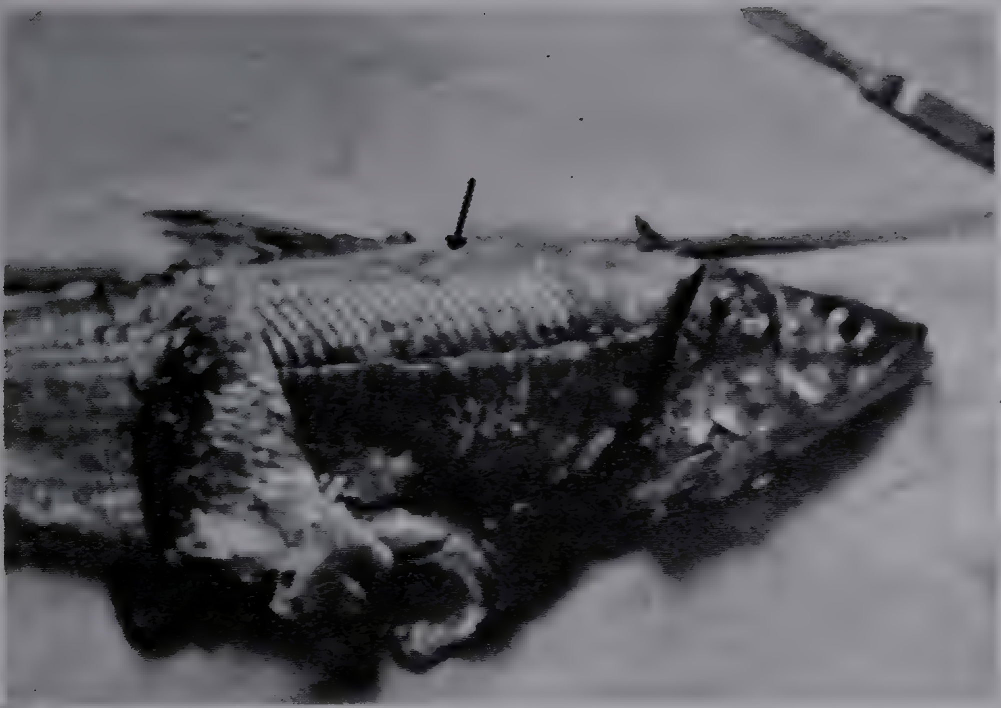
character in common—they feed largely on microscopic aquatic animals including *Cyclops bicuspidatus*. Thus the tullibee is the natural second intermediate host for *Triaenophorus crassus*. Several other fishes (whitefish and Rocky Mountain Whitefish principally) also become infested but they must be classed as 'accidental' hosts. They do not normally feed on microscopic animals but only swallow some occasionally in their 'drinking' water. They never become as heavily infested as the tullibee in the same lakes and in lakes where tullibee do not occur the parasite is also absent—a point which indicates the inability of the 'accidental' hosts to keep the cycle going.

When a tullibee swallows a *Cyclops* containing procercoids of *Triaenophorus crassus* the digestive juices soon destroy the *Cyclops* and liberate the procercoids into the stomach cavity of the fish. The procercoid sheds its now useless hooks and begins to penetrate the tullibee's gut wall. It has no hooks with which to tear a hole; instead it possesses a gland which secretes a fluid that eats away the tissues of the gut wall. This gland is visible as a small indentation of the procercoid's body at the end opposite the hooks. It can be seen in the photograph in Figure 16.

After eating its way through the gut wall the procercoid crosses the body cavity and enters the flesh of the back. By this time it has grown considerably and begins to look like a tapeworm again; it is long and slender and at one end the scolex is forming. The presence of the parasite irritates the flesh of the tullibee and causes it to form a wall around the worm. The wall completely encloses the worm and isolates it from the tullibee's flesh. When completed the wall is called a cyst and the enclosed worm the pleroceroid. Also within the cyst is a thick whitish to yellowish fluid. This consists of waste matter from the worm and broken down tissue from the host on which the parasite feeds.

Figure 19 shows a partly skinned tullibee; the arrow points to a single large cyst and also indicates the area where cysts most commonly form. Figure 20 is a photograph of a fillet of tullibee showing two cysts about natural size. Figure 21 is a photograph of a single cyst which has been cut in half and the pleroceroid pulled out.

The author has made several attempts to trace the procercoids journey through the gut wall and into the flesh but these have been only partially successful. From other observations, however, it has been possible to learn where the parasite makes the trip and when it arrives in the flesh. With regard to the first question—where the parasite penetrates the gut—the disposition of the cysts in the flesh provides a clue. They are concentrated in the muscles of the back mostly between the dorsal fin and the head. This region is most easily accessible from the stomach and would indicate that the parasites go through the stomach wall; the fact that more cysts occur on the right side of the fish than on the left also suggests that they start out from the stomach since this organ is slightly inclined toward the right side of the body cavity. Finally, clinching the argument, several plerocercoids have been found encysted on the outer wall of the stomach. Evidently a few parasites tire of the journey and encyst before they reach the flesh.



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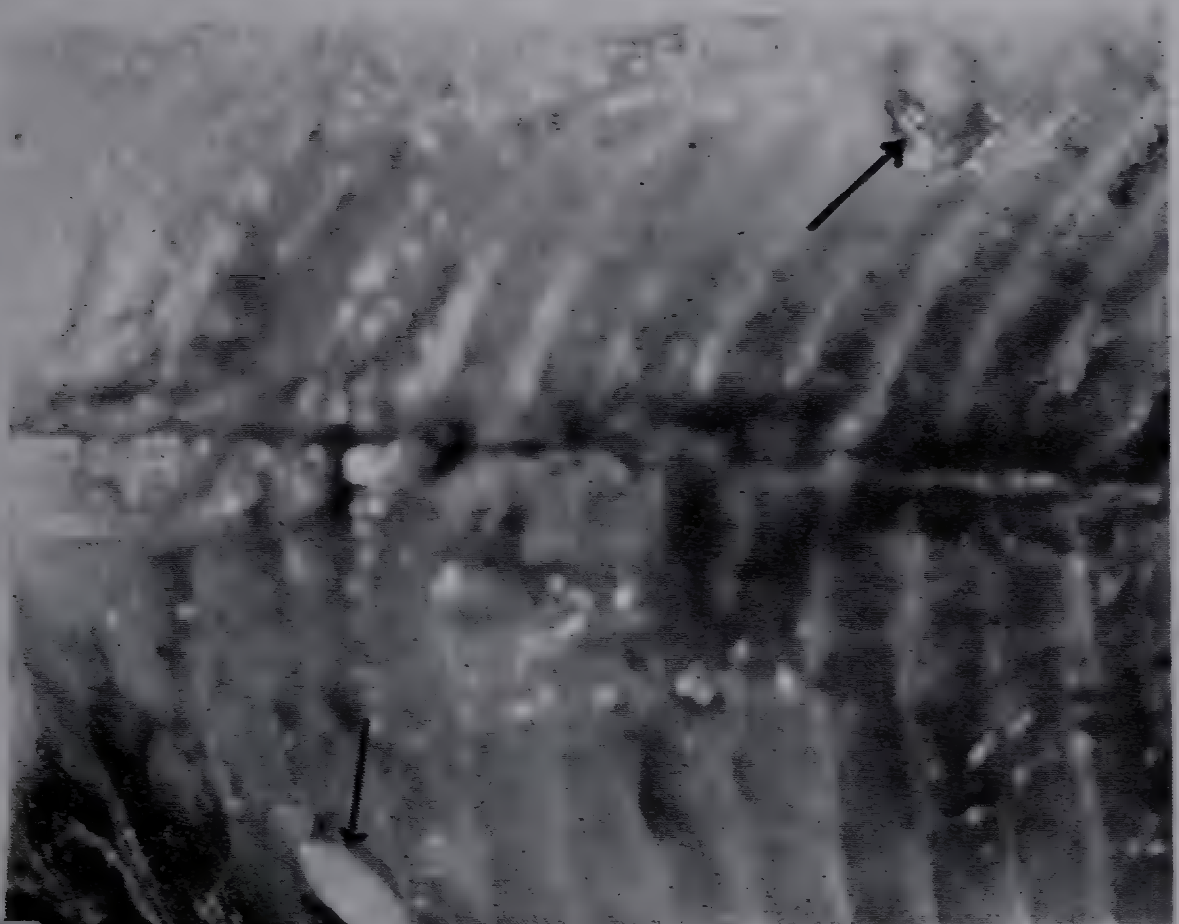

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Figure 19. A partly skinned tullibee to show region where cysts occur. The arrow indicates a single large syst. About one third natural size.

Figure 20. A fillet of tullibee with two systs showing (indicated by arrows). Natural size.

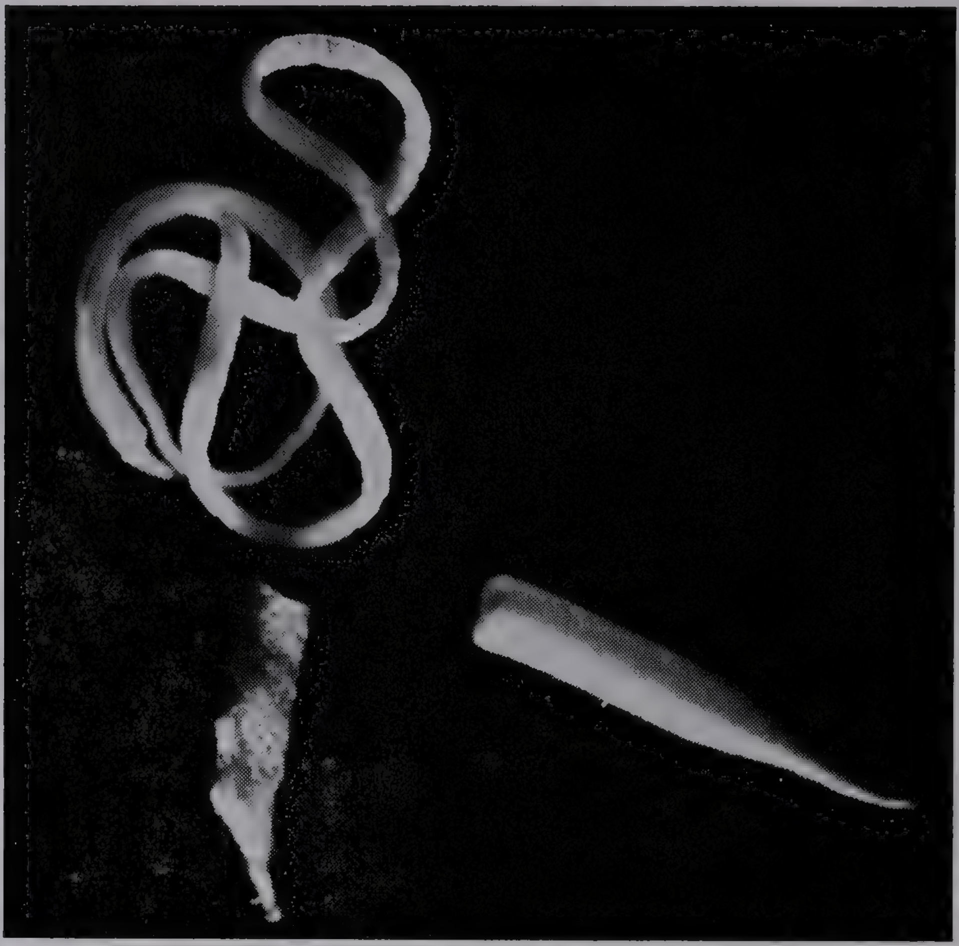

Figure 21. A cyst of *T. crassus* dissected out of a tullibee. The cyst has been cut in two and the plerocercoid pulled out. The scolex of the plerocercoid can be distinguished. Compare with Figure 1. Enlarged four times.

The problem of when the parasites reach the flesh was quite easily solved. A careful count of the number of cysts in tullibee of each age at Lesser Slave Lake was kept throughout the year. A large jump in the numbers of cysts took place in July; this increase must be due to the arrival of the new generation. The process of penetrating the stomach and encysting in the flesh must, therefore, occupy a month to six weeks as the new cysts are found this length of time after mature procercoids are first present in the *Cyclops*. The whole period from egg laying to encystment thus requires two to three months—from some time in May to some time in July.

The plerocercoid in its cyst is very similar to the adult worm in the jackfish. The scolex is identical and is provided with the four characteristic hooks. The strobila is more slender and lacks sex organs. When a jackfish swallows a tullibee containing these cysts the process of digestion soon liberates the plerocercoids. When they reach the part of the pike's intestine just beyond the stomach they start working their scolices into the intestinal wall. Within two days from the time they are swallowed they are quite firmly attached. By the following spring they have reached full size and maturity; they lay their eggs in May, leave their hosts and die.

We have now traced the complete life history; we began with the adult in the intestine of the jackfish and we have ended with the same. There is one aspect of the story about which more needs to be said; this is the time spent in the cyst stage in the flesh of the tullibee. How long can the worms live in these cysts and what happens to them if they are not swallowed by a jackfish?

If one carefully examines each cyst in a seven or eight-year old fish a great deal of variation will be found. Some of the cysts are thin-walled, large and filled with a pale coloured fluid; the plerocercoid is long and of uniform diameter throughout. Other cysts are smaller, full of thick yellowish to orange liquid and small gritty particles; the plerocercoid from such a cyst is often bloated and irregular at the tail end. In still other cysts only the scolex of the plerocercoid may be found, or perhaps no trace of the worm at all. These variations have been interpreted as indications of age. The youngest cysts are those with the pale contents and the long regular worm; older cysts become yellow or orange and the worm begins to degenerate from the tail end. The gritty particles are calcium carbonate. Some cysts eventually are converted to tiny, hard, calareous nodules; others are completely absorbed by the flesh and disappear entirely.

The study of the cysts has revealed then, that they do not live forever, but gradually degenerate and become absorbed by the host. There is evidence to tell us how long this takes. Tullibee become more heavily infested each year, until their sixth year. After that increases are slight or do not occur at all. This means that by the time the tullibee are in their sixth year the cysts must be disappearing in the flesh as fast as new ones arrive. Tullibee seldom acquire any cysts until their second or third summer. The cysts disappearing in the sixth year are therefore probably about four years old and we can assume the cysts live for four years. If we in some way miraculously killed all the tapeworm eggs in the spring we would have to repeat the operation for four years before all the reserve of cysts would be used up and the parasite eliminated.

The account of the life history outlined in this booklet has taken several years to work out and in certain details is not yet complete. The knowledge gained has done nothing to reduce the number of parasites in the fish. But it would be folly to start on a control programme without a knowledge of the life history, so this work is a necessary preliminary for any practical remedial measures which migh be undertaken. Possibilities of control suggested by the life history have been outlined in another Alberta Government booklet entitled "Suggestions for experiments in the control of the Pike-Whitefish tapeworm, *Triaenophorus crassus.*"